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The Ecology and Migrations of Sea Turtles, 2
Results of Field Work in Costa Rica, 1955

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The present paper is a summary of results of a season's field work at the green turtle *(Chelonia mydas mydas)* rookery at Tortuguero on the Caribbean coast of Costa Rica. Most of the information was obtained through work at the beach during July and August, 1955. This is supplemented by observations made in previous seasons at Tortuguero and elsewhere. The work was supported by a grant from the National Science Foundation (G-1684) and will be continued during two more nesting seasons. Results of a study of green turtle populations of the Gulf coast of Florida, a part of the same general program of research, are given elsewhere (Carr and Caldwell, 1956).

Tortuguero, or Turtle Bogue as it is known in Caribbean English, is a 24-mile extent of unbroken sand beach on the Costa Rican coast between Puerto Limon and the Nicaraguan frontier, extending from the mouth of the Tortuguero River to that of the Parismina (Reventazón) River (fig. 1). It is widely known through the Caribbean as a nesting ground of the green turtle and is thought by many to be the only remaining breeding site of any importance to the maintenance of the species in the Caribbean. While this may not be wholly true, Tortuguero is almost certainly the only rookery of significance anywhere on the mainland Atlantic shores of Central or South America, and it was for this reason that

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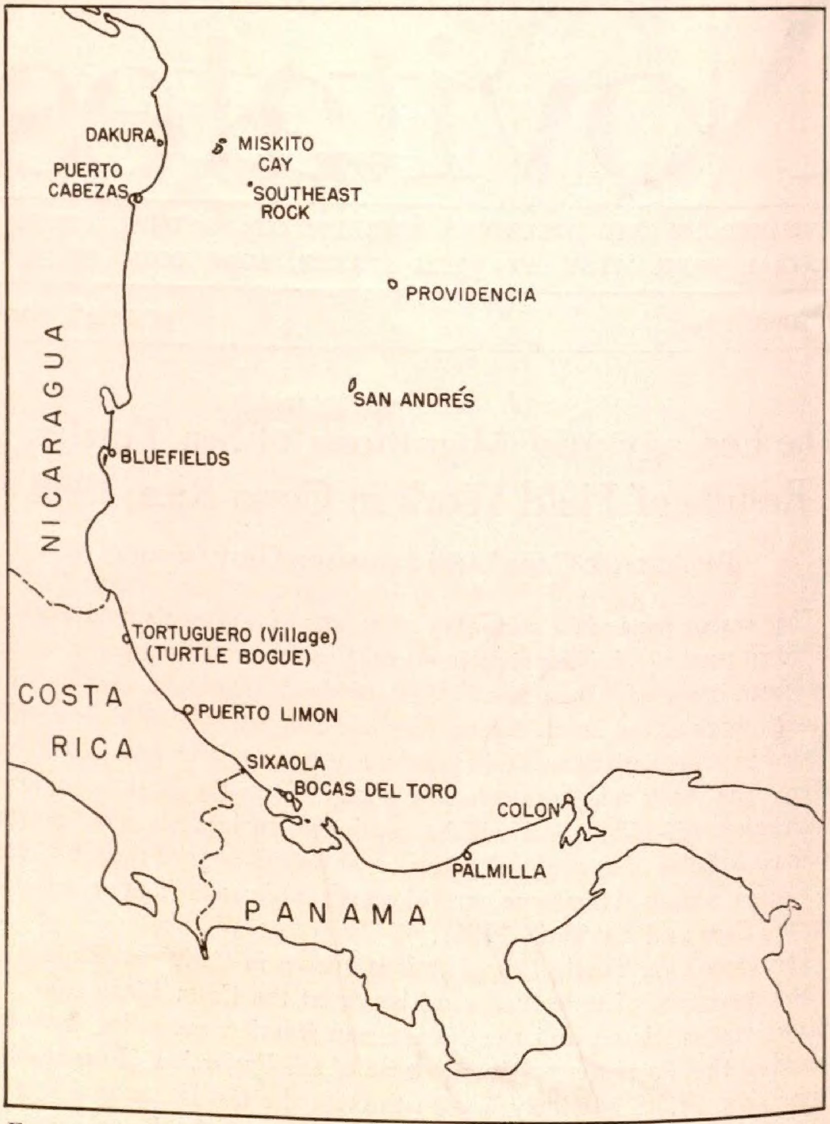

FIG. 1. Map showing western Caribbean localities involved in the tagging program.

it was chosen as the locale for a tagging program (figs. 2, 3; see also Carr, 1954a, 1954b, 1956).

After reconnaissance during three preceding summers, we set up a tagging camp on July 1, 1955, in the little settlement of Tortuguero, in a *manaca* shack furnished by Señor Teodoro Quirós C., of the Atlantic Trading Company, which takes out timber and bananas from the hinter-

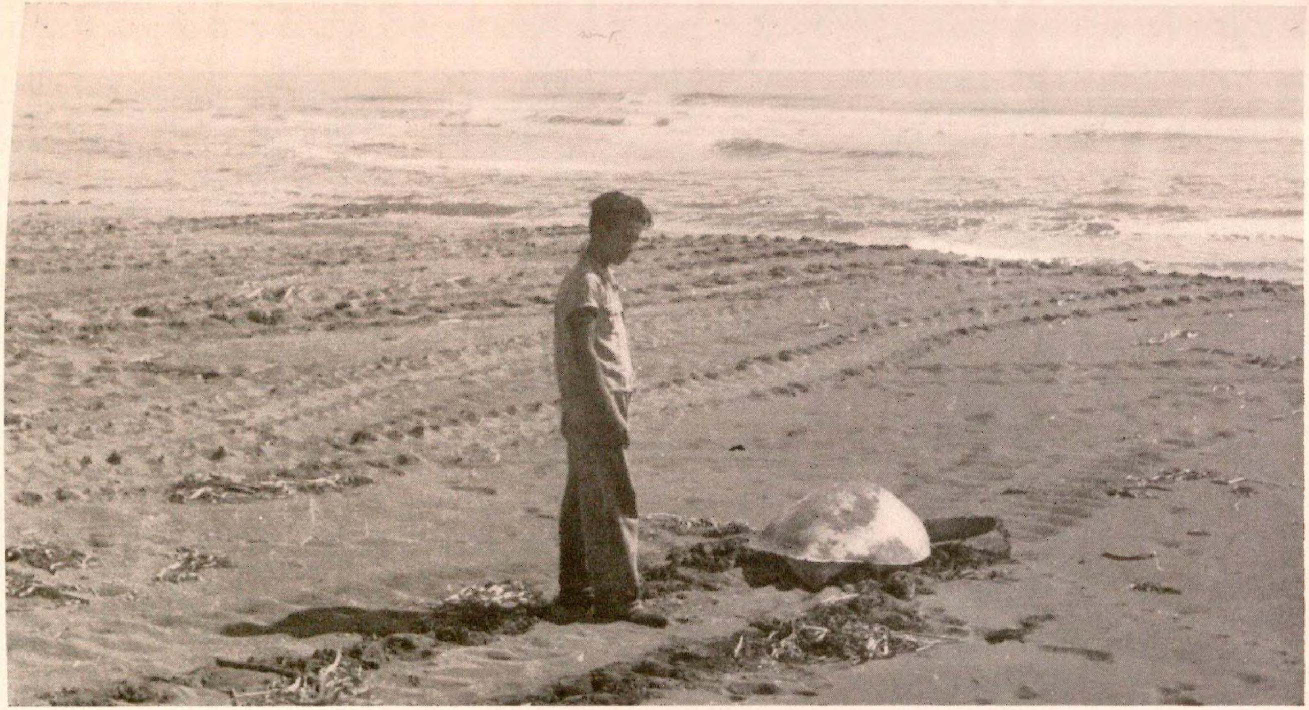

FIG. 2. A section of Tortuguero Beach, Costa Rica, showing evidence of heavy use by nesting green turtles.

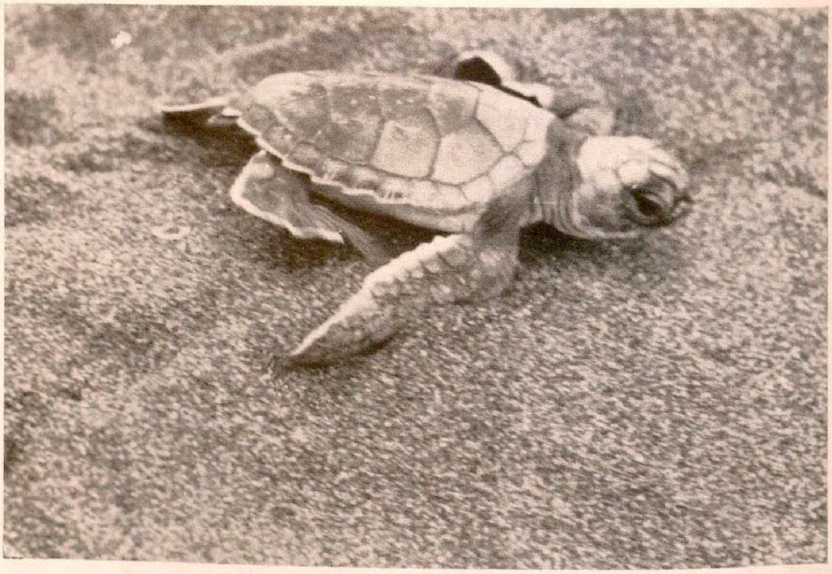

FIG. 3. A hatchling green turtle, newly emerged at Tortuguero, Costa Rica, and heading for the surf.

land by way of the Tortuguero River. We were allotted a 2-mile section of the beach adjacent to the camp, on which commercial interference was excluded, and we retained local good will by hiring for our own work the men who usually turned turtles on these 2 miles for export interests in Limon.

Turtles turned at night by these *veladores,* as the beach-watchers call themselves, were tagged and released, where caught, the next morning, all the catch of a night usually having gone back into the water by midday if not much earlier (fig. 4). In the case of each turtle tagged, straight-line measurements of the length and width of the shell were made, the point of capture was recorded as exactly as possible, and the postocular scales of each side were counted.

Two kinds of tags were used during the summer. One of these was a monel metal elliptical disk with perforations at the ends for wiring to the after edge of the shell (fig. 5). This was used for all turtles except 40 marked during the last two days of the field work (August 25 and 26). These latter were tagged with standard "cow-ear tags" of monel metal, clamped through punched holes in the thin, tough after-edge of the upper part of the front flipper, as suggested by J. R. Hendrickson[1] in

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[1] Not by Tom Harrisson, as stated by Carr and Caldwell (1956).

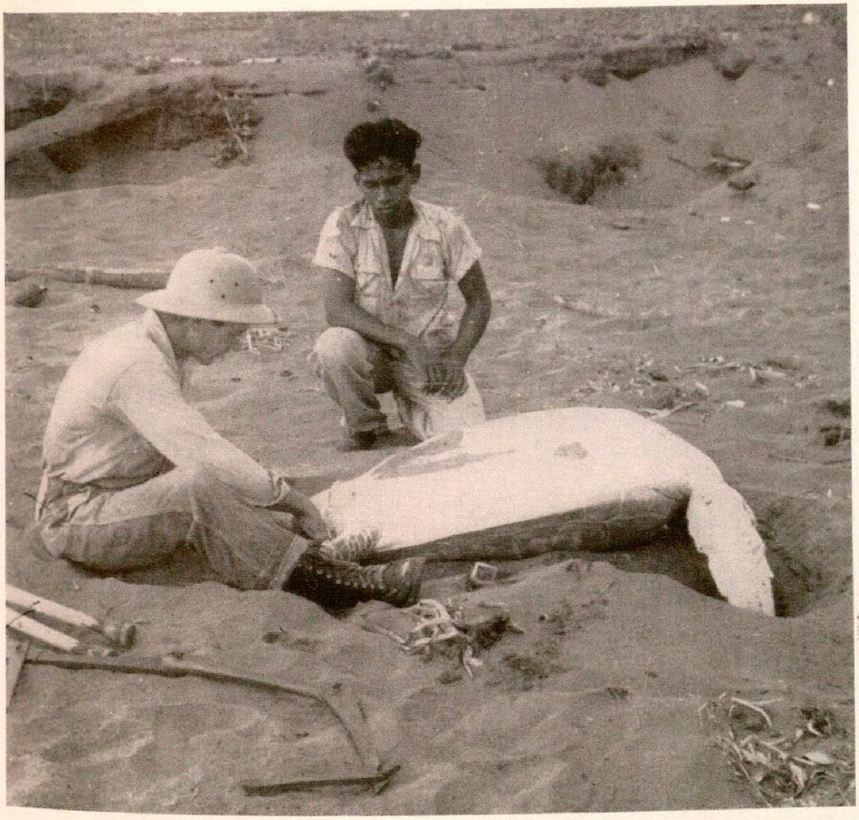

FIG. 4. Giovannoli and an assistant tagging a green turtle by the shell-tag method later discarded in favor of a flipper tag.

a paper read at the 1955 meetings of the American Society of Ichthyologists and Herpetologists. This type of tag is now being used exclusively.

Both kinds of tags were numbered and inscribed in English and Spanish with an offer of a reward for their return and with the address of the Department of Biology of the University of Florida.

During the period of the work Giovannoli was in residence at the camp from July 2 to August 29, and Carr was present for two four-day periods (when the camp was opened and closed). Six hundred and forty-four turtles were caught—or, rather, turtles were caught 644 times, 149 of the captures having been recaptures of tagged individuals that returned to the beach, 44 of which returned for two recaptures, seven for three, and two for four. Since the camp was closed, we have had 10 returns, all from outside Costa Rica. Details and implications of the data thus secured are discussed in the following pages. All turtles involved in the study were

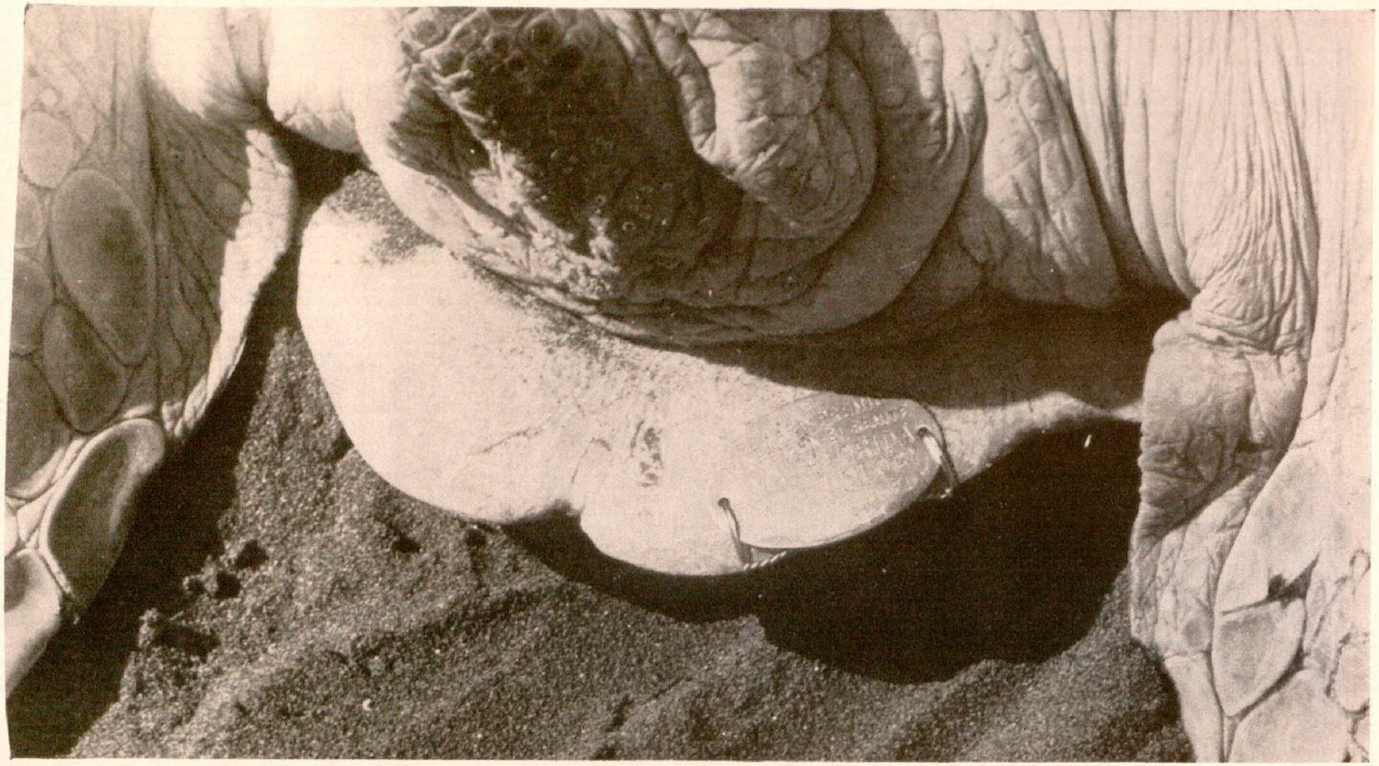

FIG. 5. Ventral view of after-edge of shell of green turtle, showing tag wired in place. This rig will apparently not often withstand the scrapings and clawings that attend pairing and has been abandoned in favor of a cow-ear tag on the fore flipper.

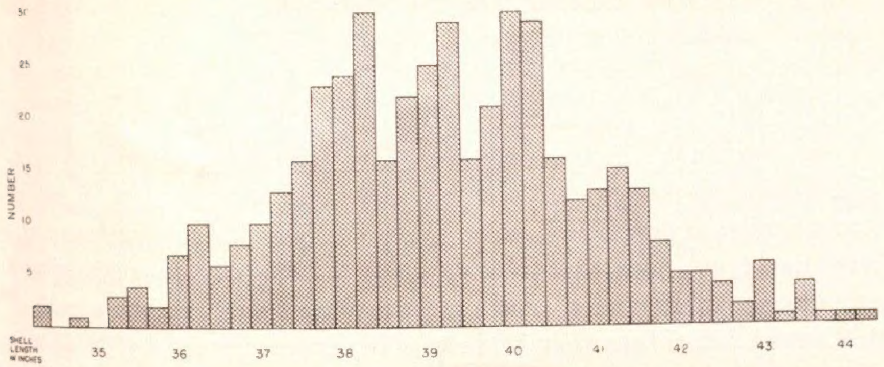

FIG. 6. Shell lengths of 362 mature female green turtles measured on the nesting beach at Tortuguero, Costa Rica, between July 2 and August 25, 1955.

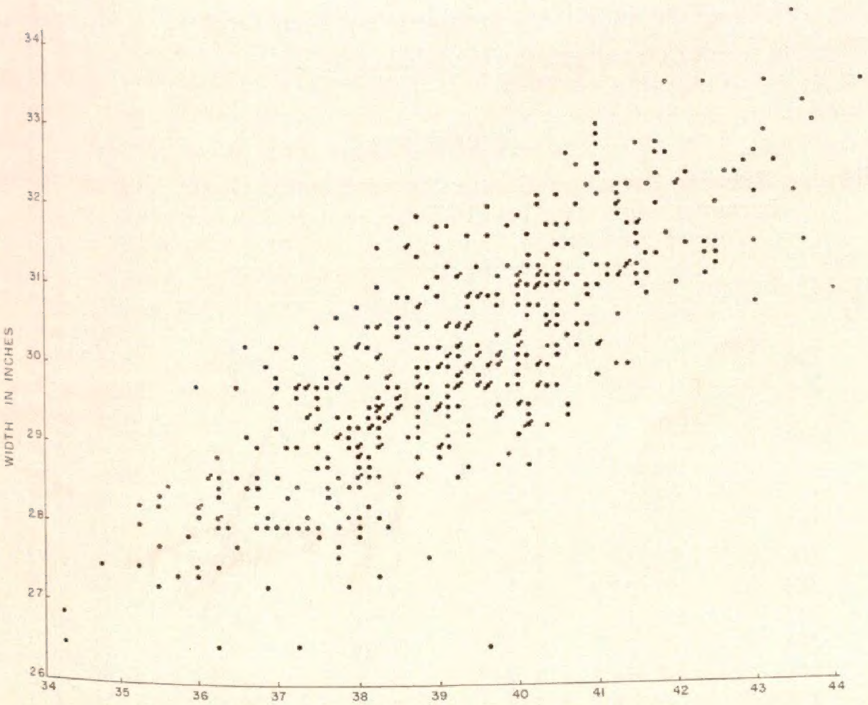

FIG. 7. Length-width relationship in sexually mature green turtles. The diagram includes all turtles measured at Tortuguero, Costa Rica, during July and August, 1955. Each dot represents a turtle. The small dots actually lie on the points covered by the large dots that they touch.

mature females, the range in size and proportions of which is shown in figures 6 and 7.

TAGGING RESULTS

The chief aim of the Costa Rican tagging program was to get information bearing on the question of mass, long-distance migrations. Pending accumulation of direct observation of schools traveling the high seas, the most direct and valuable data would seem to be those from released and recovered marked turtles. In the present project we have had a total of 149 recoveries of tagged individuals. These recoveries are of two very divergent kinds: recaptures of females that returned to Tortuguero beach within one to 35 days after being tagged, for the purpose of carrying out interrupted nesting or of nesting again; and recaptures by net or iron at points distant from the nesting beach, and clearly after the season's nesting activity of the individual involved had been finished or abandoned. Tagging results are summarized in tables 1 to 5.

TABLE 1

RETURN RECORDS INVOLVING SINGLE RECAPTURES OF GREEN TURTLES AFTER INTERVALS OF FROM 11 TO 16 DAYS, IN A 10-MILE SECTION OF TORTUGUERO BEACH, COSTA RICA, SOUTHEAST FROM THE MOUTH OF THE TORTUGUERO RIVER

Tag No.	Place Tagged[a]	Date Tagged	Date Retaken	Place Retaken[a]	Distance (in Miles) Between Sites of Emergence
313	NW. 3	8/4	8/14	NW. 3	Same place
102	NW. 4	7/3	7/15	SE. 3	1/4–3/4
124	SE. 3	7/7	7/19	Mid 2	1 1/2
105	SE. 1	7/26	8/7	NW. 2	1/2
324	SE. 2	8/5	8/17	NW. 2	1/2
381	SE. 1	8/11	8/24	SE. 1	1/4[b]
382	SE. 1	8/11	8/24	SE. 1	1/4[b]
466	SE. 2	8/14	8/24	Mid 1	3/4
126	NW. 1	7/7	7/21	NW. 3	1 3/4–2
277	SE. 3	7/18	8/3	SE. 2	1
295	NW. 3	7/19	8/3	Mid 3	1/8

[a] Numbers in these columns represent miles from northwest to southeast; letters indicate approximate portions of individual miles.

[b] Note similarity of records.

Data from Local Returns

Clumped Returns: While the local returns, of which, as noted above, we had 149 in 1955, are of interest mainly for their bearing on individual orientation and on the natural history of nesting, they should also be examined for any possible clues bearing on schooling or group movement. The most direct evidence of this sort would be clumped retakes of turtles that had been tagged together. Although the word "together" as thus used is clearly relative, there are nevertheless to be seen in tables 1 to 3 and in the case histories numerous examples, which range from the suggestive to the virtually conclusively demonstrative, of associative movements. That is to say, if turtles tagged at the same place and time are after long intervals retaken together (especially if they are retaken together at another place) and if the coincidence is not attributable to chance alone, then the turtles clearly moved together in the interim, and by extension perhaps in the migration that brought them to the beach to start with. Admittedly our cases do not add up to imposing statistical stature, and the numerous factors involved make both the application and the interpretation of probability tests pointless. But when viewed against the agreement of our case-history results with widespread lore of professional turtle hunters, the implications seem noteworthy.

As an example, the following case of clumping may be pointed out (the

TABLE 2

Return Records Involving Single Recaptures of Green Turtles After Intervals of 20 Days or More, in a 10-Mile Section of Tortuguero Beach, Costa Rica, Southeast from the Mouth of the Tortuguero River

Tag No.	Place Tagged[a]	Date Tagged	Date Retaken	Place Retaken[a]	Distance (in Miles) Between Sites of Emergence
259	NW. 3	7/14	8/16	NW. 2	1
273	Mid 1	7/16	8/16	NW. 2	½–⅝
254	SE. 10	7/12	8/10	Mid 1	9
204	Mid 2	7/12	8/7	NW. 2	¼ or less
153	Mid 2	7/22	8/14	SE. 1	⅝–¾
314	Mid 2	8/4	8/24	Mid 1	1
			8/25	NW. 3	1¾
307	SE. 2	8/3	8/24	NW. 3	¼–⅜

[a] Numbers in these columns represent miles from northwest to southeast; letters indicate approximate portions of individual miles.

TABLE 3

RETURN RECORDS INVOLVING TWO OR MORE RECAPTURES OF GREEN TURTLES IN A 10-MILE SECTION OF TORTUGUERO BEACH, COSTA RICA, SOUTHEAST OF THE MOUTH OF THE TORTUGUERO RIVER

Tag No.	Place Tagged[a]	Date Tagged	Date Retaken	Place Retaken[a]	Distance (in Miles) Between Sites of Emergence
170	SE. 1	7/9	7/11	Mid 2	¾
			7/21	NW. 3	¾
420	Mid 1	8/12	8/12	SE. 2	1¼
			8/24	NW. 3	¼ or less
405	NW. 3	8/12	8/12	SE. 1	1¼-1/12
			8/24	SE. 2	¾
265	SE. 2	7/19	8/3	Mid 2	⅜
			8/8	Mid 2	Same place
255	Mid 2	7/14	8/3	Mid 1	1
			8/5	SE. 1	¼
167	SE. 2	7/10	7/12	Mid 3	¾
			8/3	Mid 2	1
137	SE. 2	7/8	8/11	NW. 1	1½
			8/12	NW. 1	Same place
205	NW. 4	7/19	8/14	SE. 1	2½
			8/16	NW. 3	1½
206	SE. 1	7/12	8/8	SE. 1	¼ or less
			8/9	Mid 1	¼
263	NW. 3	7/16	8/10	Mid 3	¼ or less
			8/11	NW. 2	¾
390	Mid 1	8/11	8/12	Mid 2	1
			8/23	NW. 1	1¼
413	NW. 1	8/12	8/23	NW. 1	Same place
			8/24	SE. 1	½
314	Mid 2	8/4	8/24	Mid 1	1
			8/25	NW. 3	1½
190	SE. 1	7/11	7/15	Mid 1	¼ or less
			7/18	Mid 1	Same place
			8/11	SE. 1	¼ or less
394	NW. 1	8/11	8/11	SE. 2	1½
			8/12	SE. 2	Same place
			8/16	NW. 2	¼
			8/18	SE. 1	¼
383	SE. 1	8/11	8/11	SE. 1	Same place
			8/12	NW. 1	¼
			8/13	Mid 3	2¼
			8/24	SE. 1	2[b]
448	SE. 1	8/13	8/23	SE. 1	Same place
			8/24	Mid 1	¼

[a] Numbers in these columns represent miles from northeast to southeast; letters indicate approximate portions of individual miles.

[b] Same place as first emergence.

numbers used are tag numbers of turtles marked; further details of their history may be seen in the tables):

Numbers 381, 382, 383, and 393 were tagged on August 11, all within an extent of a quarter of a mile or less. All were retaken 13 days later, on August 24, as follows: No. 381 about 2 miles from the tagging site; No. 393 about 1 mile from the tagging site and 1 mile from the point of emergence of No. 381; Nos. 382 and 383 at the place where all were tagged, or no farther than one-quarter of a mile from it.

Numbers 405 and 420 were tagged on August 12 (one day after the above-named group), and all were retaken with them on August 24 on the same 2-mile extent of beach.

The explanation for the return of a turtle to the beach is discussed in the section on multiple laying. The above-mentioned turtles probably nested successfully on or shortly after the date they were tagged and released, then came back to lay again on August 24. Such reappearances at the original point of emergence as the above, and as those shown in the tables, seem obviously indicative of some sort of orientation accomplishment. It is not clear, however, how imposing the feat of orientation has been. It is conceivable that the days, or weeks, between emergences were waited out loafing or courting in the open sea off shore, adjacent to the nesting site. This, however, seems unlikely. The shore is completely exposed, with strong long-shore currents and heavy surf and with few feeding flats or sleeping rocks available. Reconnaissance by small airplane shows no great accumulation of females such as would occur if every female there for a two- or three-stage nesting venture waited around during the periods between her trips ashore.

It seems more reasonable to suppose that between times the turtles depart for areas about the mouths of rivers up and down the coast, where bars and shallows afford both protection and vegetation for food. If this is the case, the returns to precisely located points on the nesting beach become feats of greater stature.

While the many variables that must have been coordinated in the accomplishment of these localized reappearances seem to rule out chance, it should nevertheless be noted that extremely divergent cases were recorded, in which returns to the beach occurred as far as 10 miles away.

Time, Distance, and Direction in Recaptures: An effort was made to augment the direct evidence for associative movement obtainable from case records by a tabulation of the time and distance between recaptures and the direction of the site of recapture from that of release. It not only seemed of interest to know whether turtles, on visiting the beach a second time, showed a tendency to come out near the point of their first emergence, but also whether emergences *not* near points of release showed any associative trends in distance, time, and direction that might quantitatively bolster the more striking individual cases. If second and later emergences generally proved to show no relation to the original site, we wanted to see whether they tended to group elsewhere, or at least to occur northward or southward of release points. Such trends might be interpreted, cautiously, as indications of group long-shore movement which might be part of, or of the quality of, seasonal migratory movement.

Table 4 shows the sort of analysis that might be expected to reveal such movements. The fact that it fails to show any arresting trends may merely be due to the small sample that remained for such treatment after the weeding out of ineligible cases. Most of our work was done on the first 3 miles (northernmost miles) of the beach, and the eccentric position of this site made it necessary to throw out all returns for individuals tagged there (except for some of those included in the zero column) in this analysis. The restriction of the sample to turtles tagged towards the middle miles of the beach left only the 60 returns tabulated north and south of the zero column.

Data in the zero column itself have little bearing on movement but are most striking evidence of orientation capacity and perhaps of a special kind of "homing" ability, as the 36 individuals listed there all came back to a section of beach less than a mile long—many of them to within a few hundred yards of the site of their first emergence.

COUNTS AND MEASUREMENTS

In addition to the clues and evidence available in the tag returns, indications of school movement might be expected to appear in seasonal changes in counts and measurements made on emerging turtles, providing characters involved in school-specificity could be found. Our efforts in this line were exploratory and unproductive, but we do not believe that the fact that our data on the postocular scales show no definite secular trends rules out the desirability for continuing a search for characters suitable to this sort of inquiry.

There seems to be no reason why traits could not be found that announce the arrival of separate schools because each school is slightly more of a stamp with respect to that trait than it is like any other school. There is strong circumstantial evidence that (1) turtles arrive at Tortuguero in schools, (2) schools arrive at different times, and (3) some, at least, of the schools come from different and separate home (feeding-sleeping) ground north and south of the Tortuguero nesting ground. The suggestions of concurrent emergence behavior shown elsewhere in this paper may be attributable to school cohesion by such variously derived groups. There also seems to be the possibility that, because of the completely herbivorous, herd-grazing habits of the green turtle its populations are broken genetically into demes, which, because partly isolated from other similar populations, may acquire measurable differences from them.

It might be objected that the isolation on the separate feeding ground can be of no evolutionary importance, because, theoretically at least, the schools all repair to a common breeding center, where not only egg laying occurs but also the pairing off and copulating that might be expected to mix the gene pools of whatever groups were concurrently present and not only overcome any drift effect but also dilute any selective effects produced in the populations by differences in conditions in their home areas.

Opposing this objection, however, is the likelihood of separate, synchronous periodic action by the different schools, the members of each of which, reacting to the same set of periodic factors, depart for the nesting ground simultaneously and thus on the whole tend to mate with one another more often than they mate with members of any other school. This effect would be reënforced by the fact that copulation in green turtles occurs just before or just after oviposition (see section on Natural History of Reproduction), with the males closely attending the nesting females, following them into the surf on the way ashore or catching them the moment they are afloat on their return. (Harrisson, 1954, and our own observation.)

It seems unreasonable to suppose that these rutting males would be any more inclined to mount a female of their own population than one from a concurrently present population from a different source. But the schooling tendency would nevertheless tend to increase the relative frequency of intrapopulation matings, and with time this would inevitably result in differences in gene frequencies. The only question is whether these differences are morphometrically detectable.

Postocular Counts: One of the most promising variables with which to test for differential school "makeup" seemed to be the number of postocular scales (the big scales that form the hind rim of the orbit and in the species range in number from two to five). The modal and greatly predominating number counted was four on both sides. As table 5 shows, the range in our data was from three to five, with asymmetry more frequent than symmetry in the non-modal counts. It was hoped that any incipient population divergence that might exist would appear as seasonal clumping on an average basis. But, as table 5 shows, the 4-4 count is so

TABLE 4

Tag Returns for Tortuguero, July–August, 1955, Showing Relation Between Time, Distance Traveled, and Direction of Site of Recapture from Site of Release

Days	Miles South of Point of Release				Miles North of Point of Release		
	3–10	2–3	1–2	0[a]	1–2	2–3	3–10
1–5	7	4	18	18	11	4	4
5–15	1	1	2	11	4	1	0
15–25	0	0	0	4	2	0	0
25–35	0	0	0	3	2	1	1

[a] This does not represent a fixed point on the beach but rather any point within the 10 northwesternmost miles where turtles were released and from which recovery distances were measured. Only cases in which the sites of release and recovery were precisely known are included.

TABLE 5

Postocular Scale Number, Total and Monthly Frequencies, in 493 Green Turtles, Tortuguero, Costa Rica, 1955

	3-2[a]	3-3	3-4	4-4	4-5	5-5	3-5
Total	5	25	30	362	48	22	1
July	1	10	18	166	26	9	0
August	3	15	12	198	21	13	1

[a] Counts for the left and right sides, respectively.

much the most frequent that our samples of all the aberrant counts were small, and no significant seasonality could be detected.

Seasonal Length-Frequency: Another variable, in which we met with more success in finding significant seasonal trends, was shell length. School differences in this character may, of course, not be genetic at all but merely indicative of differential richness of pasturage in feeding grounds or of differential periodicity in movements of ontogenetic groups within a single population. Admittedly, a significant seasonality in clumps in shell length lacks the sure evolutionary relevance that clumps in scale frequency would carry, but it nevertheless implies schooling of some sort, and that is the central interest of this study.

What we interpret as probably valid evidence of periodicity of size groups may be seen in figure 8.

SEX RATIO

Because of the heavy and widespread killing of female turtles during their vulnerable period on shore, a growing preponderance of males in mature sea turtle populations might be expected. Our results at Tortuguero furnish no evidence on this subject, because the observations there involve only the mature female turtles that use the rookery, with occasional sight records of males chasing females in the surf or, from an airplane, seen courting or copulating.

At the Miskito Cay fishery, however, some 300 miles to the northwest, the turtling operation is not selective with respect to sex, and the sex ratio in the net-taken catch there can probably be taken as representative.

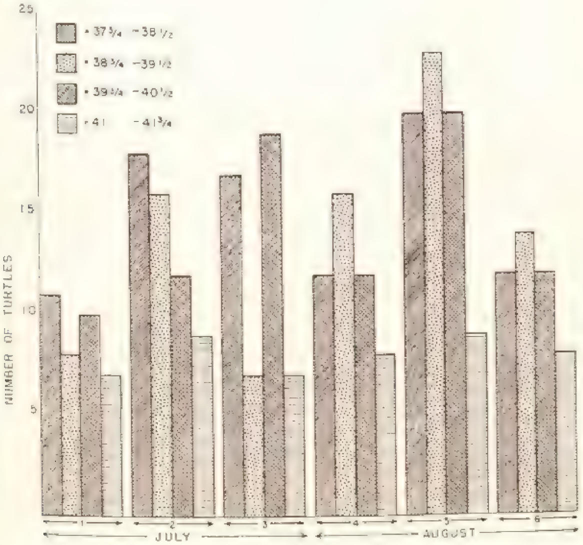

FIG. 8. Fluctuation in four somewhat arbitrarily chosen (see fig. 6) measurements (in inches) of length classes of nesting green turtles during six periods, of five collecting days each; July and August, 1955; Tortuguero, Costa Rica; miles 1–10.

We have talked about the question with a number of turtle captains and have found among them the rather surprising opinion that the sex ratio varies "from year to year." What this means, if anything, it is hard to say. The most likely explanation seems to be that it is actually "from season to season" that the proportions of the sexes are seen to change. Such changes, if they occur, might be attributable to differential scheduling of migration departures and arrivals by males and females traveling in homosexual schools.

The only direct information available comes from two cargoes of unsorted green turtles caught on Miskito Bank and carried to market, respectively, in Grand Cayman and Key West. A sex tally was made of these by Giovannoli. The two schooners involved were the "Autarus" of Grand Cayman unloading at Georgetown and the "Adams" of Grand Cayman unloading at Key West. All turtles were from the vicinity of Miskito Cay, and all were caught between February and April, 1956. Sex frequency was as follows:

	Males	Females
"Autarus"	27	66
"Adams"	105	271

Elsewhere Carr (1956) has commented on the apparent predominance of male green turtles when the sea off the nesting ground is surveyed from the air. Because any female at the surface is usually attended by two or more males, and because females not immediately concerned with nesting apparently move away temporarily, an aerial survey gives an impression of a disproportionate number of males. Such observations, however, have no bearing on the actual sex ratio, as only a small, selective segment of the breeding schools is in evidence.

Multiple Nesting

There is evidence of several kinds that the Atlantic green turtle may lay more than once during a season, as the form in the Pacific is known to do. For example, it has often been stated by those who habitually butcher green turtles that the egg complements of gravid females are often in two or more batches, of unequal size, and destined to be laid during separate emergences. Such persons and the *veladores* who turn turtles on the beaches generally agree that there are usually three such emergences in a summer and that these occur at intervals of from 10 days to two weeks. In various places about the Caribbean we have talked with turtle men who cite specific instances of a female turtle, recognizable because of some deformity or injury, that came ashore twice in "about two weeks."

It might be expected that a study such as the present one, yielding recaptures of turtles on the nesting beach where they were marked, would settle this question once and for all. Such is not the case. As we said above, the chief purpose of this year's project was the building up of a fleet of marked turtles that would allow the testing of the migration theories, and, as nearly any tagging program yields only scant returns, our efforts were all bent towards getting tagged turtles on the seas. When a turtle is found on the beach at night it is next to impossible to be sure that it has accomplished nesting, without making a laborious search back along the animal's trail for the concealed nest. The alternative is to watch an individual throughout the laying process, from emergence through oviposition. This may easily consume an hour's time (sometimes more) and meantime other turtles have gone back into the sea, tagless. While we recorded what each turtle found was doing, and what she *probably had* done, on the beach when caught, the number tagged after they had certainly laid their eggs was only six. Of these there were no recoveries.

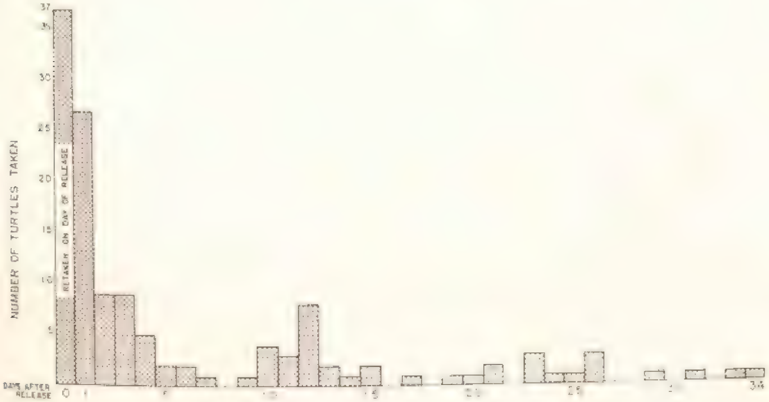

FIG. 9. Bar diagram showing frequency of retake intervals for green turtles tagged at Tortuguero, Costa Rica. It should be noted that the horizontal scale does not show calendar days but days of interval between the time of release of the tagged turtles on the nesting beach and the time of recapture there. Distance is not taken into account, but in no case were distances of more than 10 miles involved. While the sample is not large, it seems to us that the peak between 10 and 15 days and perhaps even the slight tendency to clump at the 20-26-day point should be considered in the light of the widespread belief that Caribbean green turtles lay several times a season, at intervals of 10 to 14 days.

Data on this aspect of nesting will require a special sort of tagging project in which a great deal of time is given over to determining definitely that each female tagged has finished laying. The man-hours involved in an effective project of this kind will be imposing.

Lacking direct information, we made a half-hearted effort to discover in our data quantitative hints with possible bearing on multiple emergence. We were surprised to find what appears to be support for a 13- or 14-day frequency cycle. The frequency distribution of retake intervals for our 149 recoveries is shown in figure 9. Three features seem noteworthy:

the large number of individuals retaken after only 12 to 24 hours from the time of release; the falling off to zero after about nine days and building back to a fairly strong peak after two weeks; the emergence of a suggestion of a possibly comparable peak after 20 to 25 days.

There can be little doubt that the predominance in figure 9 of intervals of only a few hours indicates reëmergence to accomplish nesting interrupted by capture at the time the tags were put on. As to the two rudimentary peaks at successive 12-day intervals, the temptation is of course to see in them corroboration of the fishermen's three-stage laying (12-day intervals and all). Although the much vitiated sample in which the peaks occur greatly reduces their significance on a purely statistical basis, it is not clear how the mutual relation between the three peaks reënforces the probability that the peaks represent actual cycles.

International Returns

The Costa Rican tagging project was set up, as explained above, as one aspect of a broad program to trace movements of sea turtles. It was suggested by, and specifically designed to test, two hypotheses, derived from circumstantial evidence and from the widespread beliefs of Caribbean fishermen, as follows:

1. The Tortuguero rookery is the main nesting ground for the big resident green turtle populations of the Miskito Cay area—the bars and flats of Miskito Bank, some 300 miles northwest of Tortuguero, off the coast of Nicaragua (figs. 1, 10, 11).

2. In addition to receiving nesting migrants from this one residence area, Tortuguero is visited from some other, if not most other, sections of the western Caribbean, especially from the coast of the mainland from Panama to Venezuela.

The evidence upon which these and other related suppositions rest is reviewed elsewhere (Carr, 1956) and is not shown here.

At the time this paper goes to press we have returns from 10 of the turtles marked at Tortuguero during July and August, 1955. All returns are from either Panama (three) or Nicaragua and the Miskito Cay area (seven), and the maximum distances represented, about 300 miles, were attained by both northern and southern migrants. Results are summarized in table 6.

While these data show, for the first time, positive proof of long-range individual movement, probably the aftermath of the undertaking and culmination of the nesting migration, it is not clear how good as evidence for mass migration they are, because they can be variously evaluated quantitatively. Whether the fact that all long-range recoveries were made

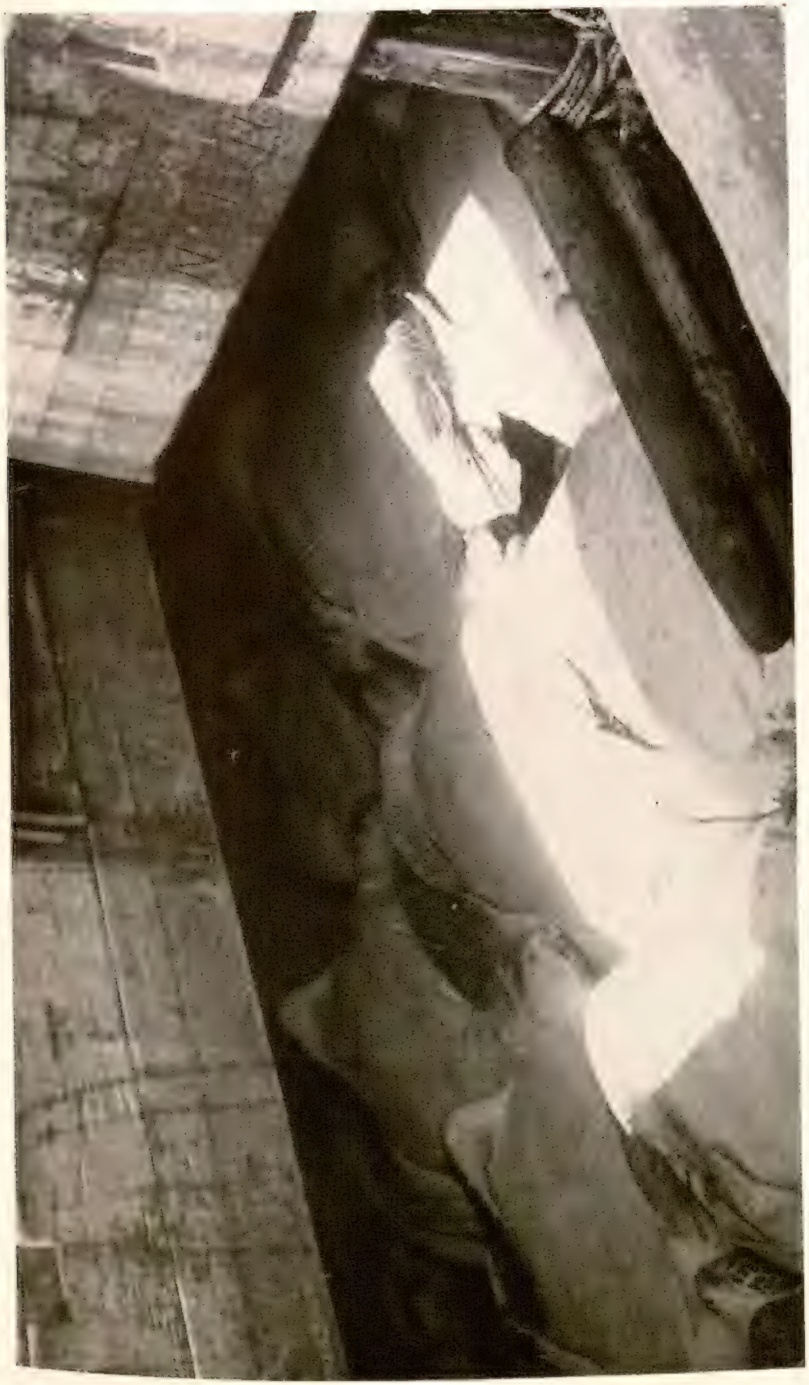

FIG. 10. Green turtles from Miskito Cay, Nicaragua, in hold of Cayman Schooner "Goldfield."

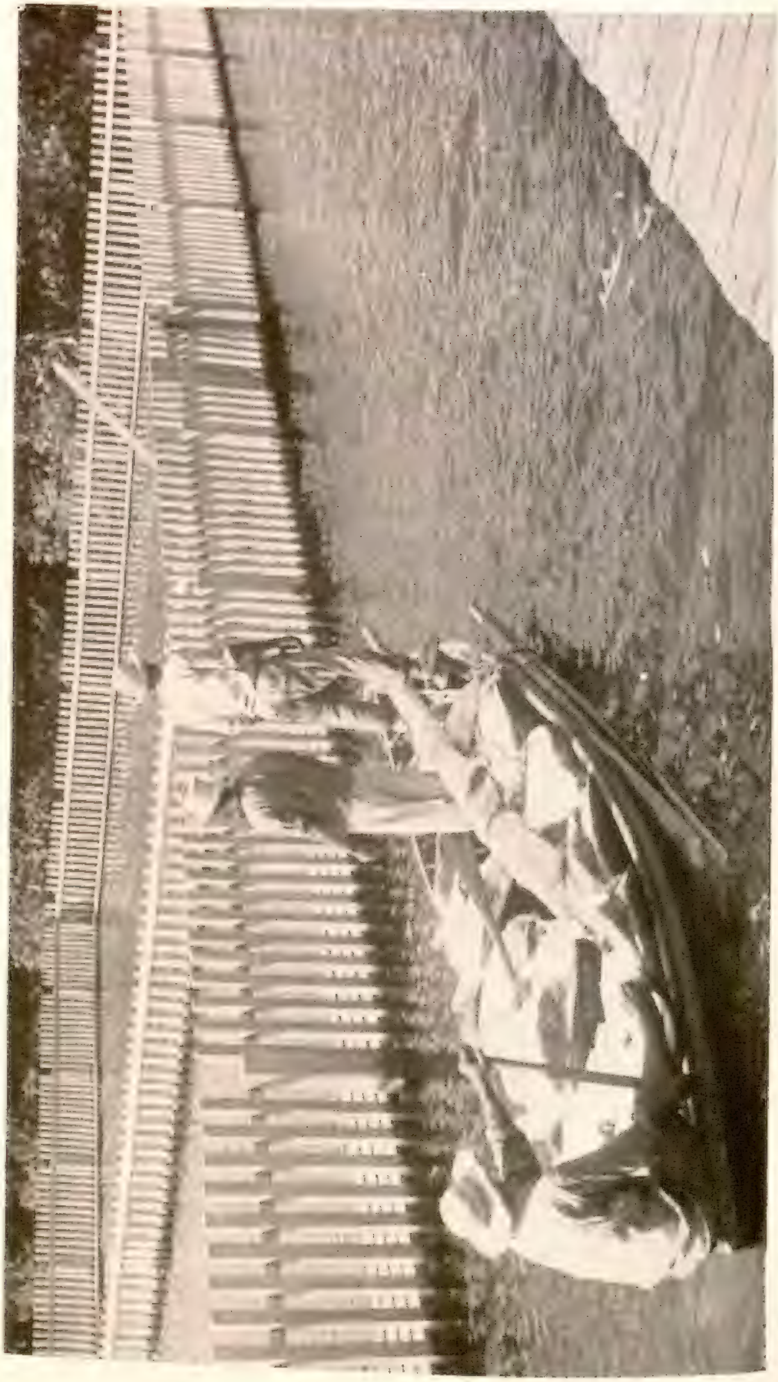

FIG. 11. Turtle "dory" with Miskito Cay green turtles from Cayman Schooner "Goldfield" about to be unloaded in crawl on Grand Cayman.

in Panama and in Nicaragua, where they were expected (none nearer the nesting beach, none elsewhere in the Caribbean), means that most turtles that leave Tortuguero after nesting go to those places and stop (return home), or whether sampling by Panamanian turtlers and by the famous Cayman schooners that catch the Miskito Cay turtles is simply the most efficient that occurs, is impossible to determine mathematically.

It is also hard to evaluate the effect on return results of the loss of tags at various periods after tagging. That heavy loss occurred is shown by the much better performance of the fin tag, of which we used fewer than the shell tag that was used during most of the program. Of 455 shell (disk) tags put on during July and August, only four came back, whereas of 40 fin tags, all put on during the latter part of the study, four also were returned. Both types of tags were among returns from both Panama and Nicaragua.

This marked disparity may partly be explained by the fact that the fin tags were used at the end of the tagging period, which allowed less time for them to be lost. The significance of this fact seems to diminish in the light of the generally much later return dates for the recovered fin tags. We have positive evidence that at least two shell tags were lost. Among the turtles of the two cargoes from Miskito Cay discussed under the section on Sex Ratio, two sets of our wire holes, unmistakably indicating lost shell tags, were found by Giovannoli.

The longest release-recovery interval was the seven months between the time tag 219 was put on at Tortuguero and the time it was taken off near the mouth of Rio Grande in Nicaragua, a point closer to the site of tagging than in the case of any of the other international returns. The only indication of speed of travel by the migrants is obtainable from the case of tag 213, the bearer of which moved from Tortuguero to a point in Panama about 300 miles away between August 24 and September 3, 1955. It is of interest that the minimum speed represented corresponds closely with the rate of travel in one of the anecdotes of homing journeys by green turtles recorded by Carr (1956).

This same individual, No. 213, was recaught on the same day and in the same place (see table 4) as No. 316, which had been tagged 19 days earlier. It is interesting to speculate whether No. 316 remained at Tortuguero and left with No. 213, perhaps both as members of a school that gathered then and traveled south in a body, or whether the two simply went back separately to a home feeding ground, or whether one or both were en route to some place even farther away when interrupted by the turtle net. This problem of homing versus migration in the interpretation

TABLE 6

LONG-DISTANCE (INTERNATIONAL) RETURNS OF GREEN TURTLES TAGGED AT TORTUGUERO, COSTA RICA, DURING 1955

Kind of Tag[a] and No.	Place Tagged[b]	Date Tagged in 1955	Date Retaken	Place Retaken[b]	Finder
Disk 483	NW. 3	8/17	9/21/55	1½ miles W. of mouth of Palmilla R., Colon, Panama	McNeill Connelly, turtle fisherman
Disk 133	NW. 3 SE. 9	7/8 7/12	Sept.–Oct./55	5 miles N. Puerto Cabezas, Nicaragua	Padre Feliciano, Misión Católica, Puerto Cabezas, Nicaragua
Disk 316	SE. 3	8/5	9/3/55	Palmilla, Colon, Panama	Julio Pinilla, school teacher
Fin 213	NW. 3	8/24	9/3/55	Palmilla, Colon, Panama	Julio Pinilla, school teacher
Disk 363	NW. 3	8/11	Sept./55	Miskito Cay	Cleveland Diego, Miskito Indian
Fin 247	NW. 2	8/25	3/14/56	14 miles SSE. Miskito Cay	Capt. Ebanks Osbert, Schooner "Autarus," Grand Cayman
Fin 219	NW. 1	8/25	5/1/56	Mouth of Rio Grande, Nicaragua	Timothy Eden, turtle fisherman
Fin 240	SE. 1	8/24	3/3/56	Southeast Rock, S. of Miskito Cay, 224 miles N., 15° E. of Tortuguero	Capt. Allie Ebanks, Schooner "Adams," Grand Cayman
Tag holes only	Tortuguero	July–Aug.	Mid-Feb./56	Miskito Cays (exact locality unknown)	Capt. Ebanks Osbert, Schooner "Autarus" (turtle examined at Grand Cayman)
Tag holes only	Tortuguero	July–Aug.	March/56	Miskito Cays (exact locality unknown)	Capt. Allie Ebanks, Schooner "Adams" (turtle examined at Key West)

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[a] See text, page 4.

[illegible]

of tagging results receives some comment in Carr and Caldwell (1956) and needs a great deal more study.

NATURAL HISTORY OF REPRODUCTION

NESTING: Although the literature contains numerous accounts of nesting by green turtles, most of these apply to the Indo-Pacific populations, and all are given in more or less general terms that furnish little of value as basis for detailed comparison with other species. The time is past when it was worth while to publish the bare statement that a given kind of turtle lays leathery-shelled eggs; that she usually lays them at night; that she lays them in a hole in sand, nearly always above high-water mark; that she digs the hole with the back flippers used alternately; that the hole is bottle-shaped and about as deep as the flipper will reach; that the hole is filled by the hind flippers; and that the site is hidden by thrashing and flinging of sand by all four feet. All these facts are merely the framework of the operation, the easily seen acts performed by all nesting sea turtles, and indeed, with minor variations, common to all modern Testudinata (except perhaps for the ridley, which appears to have no reproductive habits of any kind). It is one of our aims in the investigation now under way to record the more detailed behavior of the various Atlantic sea turtles, not only for the sake of a better understanding of the animals, but to learn, of this readily observable phase of their life histories, the degree to which they adhere to or depart from a common pattern. The process of nesting involves a complex and presumably laboriously evolved and delicately adjusted set of reactions. Once the student gains some confidence in sorting out the mannerisms as homologous behavior or mere parallel expediency, he will have gained a new sort of criterion to bring to bear on the problems of relationships among the turtles.

The present field work has afforded opportunity to make observations that justify a certain amount of comparison among the species. Carr has previously made timed, move-by-move records of the nesting of *Lepidochelys olivacea,* and the aggregate of published and unpublished data on *Caretta c. caretta* give a fairly good picture of the procedure in that form. During the past three years we have repeatedly watched nesting activity by green turtles and have recorded in detail schedules of maneuvers from emergence to return to the sea. It is against this background that we judge the performance of the individual the behavior of which is described below to be typical, and give the first account in the literature of nesting by an Atlantic green turtle.

The turtle was an individual 38⅜ inches in shell length, which was found on Tortuguero Beach on the evening of August 25, 1955. It bore fin-tag No. 227, which was put on the morning of the same day, after the turtle had been turned the night before. The return of the turtle to the beach implies that the first capture occurred before it had nested. Its coming back to lay, only 12 hours after the experience of spending the night back down on the shore, is a characteristic manifestation of the strength and "singlemindedness" of the nesting drive.

On the night the observations were made, Carr went out with the special aim of recording details of the nesting process, because, for reasons discussed elsewhere, the tagging operation affords little opportunity for the study of such details. After six turtles had been disregarded because they were already in advanced stages of nesting, No. 227 was found at 9:15 P.M., as she was emerging from the breakers about 2 miles from the point at the mouth of the Tortuguero river. By luck, she was sighted without the aid of a flashlight. The nesting urge will not often withstand the shock of a focused flashlight beam at this point in the process, the typical reaction being an abrupt return to the surf.

After a few stops to "smell" the sand (see below) the turtle dragged herself out of the water and started up the beach. The trip took her a distance of about 55 paces, and, with many pauses and periods of apparent appraisal of the outlook, consumed 20 minutes. When the turtle reached the edge of the beach vegetation (largely sea grapes at this point), she crawled uncertainly back and forth a few times, then settled herself and at 9:35 P.M. began making tentative "swipes" at the sand with her front flippers. These strokes led gradually into purposeful digging. The first operation was the thrashing out of the nesting pit (a broad depression, in this case about 4 feet wide) dug by violent throwing of sand by all four feet, the body meantime rotating slowly. As the depression deepened, the body of the turtle, or its back three-quarters, was lowered into it.

At 10:00 P.M. the turtle was well planted in her pit, the pivoting had stopped, and the deepening and enlarging of the hole continued largely by means of alternate kicking by the hind feet. At 10:16 P.M. the kicking stopped. The turtle pushed the distal edge of a hind flipper against the bottom of the pit, curled it, and scooped out the first sand from what was to become the egg cavity.

From then on the digging of the egg chamber continued for nearly half an hour, the two hind fins being thrust alternately into the deepening hole to "palm" out perhaps a teacupful of sand each time. Then a curious maneuver was observed—one not mentioned in the sketchy accounts in the literature of nesting by the Pacific form and not noticed by us during careful observance of nesting by the loggerhead turtle and by the Pacific ridley. As the working flipper was thrust into the hole for its load of sand, the other flipper was spread firmly on the sand beside the mouth of the hole. The excavating fin raised its burden of sand out of the hole, slowly moved it to the side, and dropped it. Immediately the off flipper shot out laterally and upward and struck the under margin of the shell a hard back-hand blow. There was great force in this movement, and the thumping sound it made could be heard above a moderate surf when the observer moved away to a distance of 40 paces. This mannerism is typical and is continuously executed throughout this stage of the digging. We have twice located nesting turtles in the dark by tracing the sound. The aim of the movement seems to be to rid the site of any loose sand that might fall into the cavity. The action is too fast to follow with the eye, but when such a stroke has been completed the lip and environs of the hole on the side where the flipper rested are clean and firm. As the flippers alternate in digging, the process is repeated in reverse, and the whole operation of excavating the urn-shaped egg cavity is a series of such bilateral reciprocal actions.

At 10:45 P.M. the turtle stopped digging, dropped her tail low in the cavity, and began to lay. The complement was dropped singly and by two's, the intervals between extrusions of eggs varying between one and 10 seconds except for a few periods of rest of as long as 30 to 60 seconds towards the end of the operation. Throughout the time that the eggs were being dropped, the two hind flippers were spread and held horizontally close together over the opening of the cavity, covering it completely (fig. 12). This seems to be a typical, though not invariable, maneuver, for it was noticed in every case except one that was watched at this stage of the process (at least several dozen). It is a marked departure from the behavior of *Caretta* and *Lepidochelys* which press the vertically oriented back fins against the upper part of the wall of the cavity as if to keep sand from falling in.

At 11:08 P.M. laying was completed, and the filling of the egg hole was begun (fig. 13). The turtle reached laterally with alternately working hind flippers, raked in sand, and kneaded it into the hole. When the hole was full the raking and packing continued, so that the mound grew beneath the after edge of the shell. From time to time the turtle bunched and squeezed this mound between her flippers, and as it continued to grow the back end of her body was pushed up until it was nearly horizontal, instead of being inclined on the slope of the nest pit as it had been throughout the laying process.

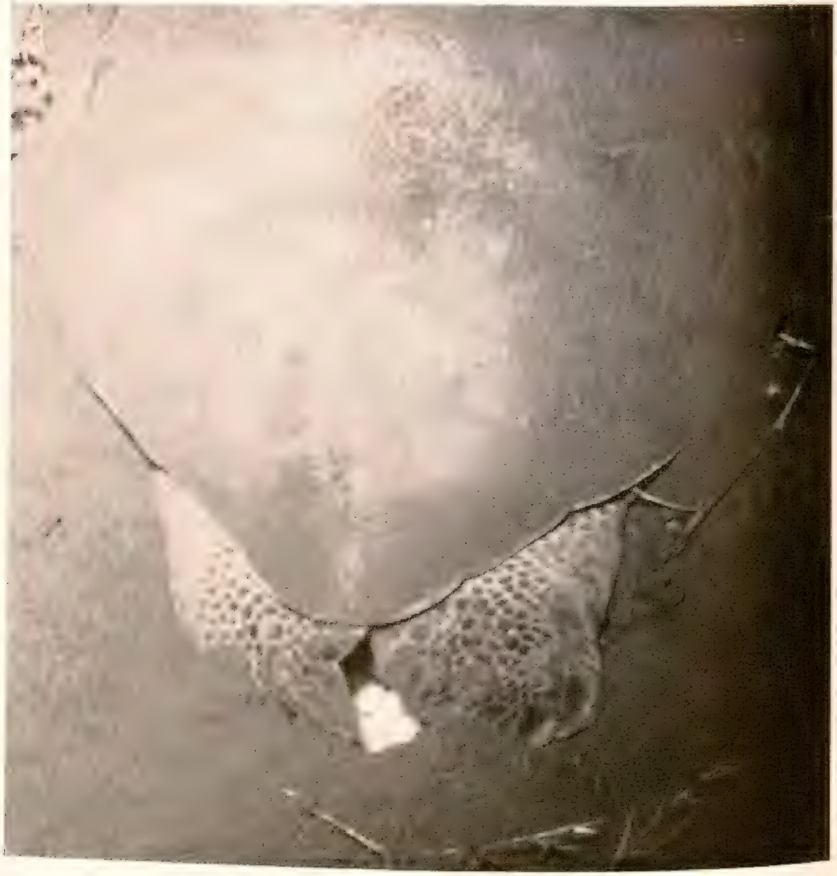

FIG. 12. Posterior view of green turtle in process of laying, showing characteristic covering position of the spread hind feet, here pulled slightly apart to show eggs.

At 11:15 P.M. work with the hind flippers stopped and the fore fins began to thrash and to sling sand. After a few strokes, the hind flippers joined in this work. As the turtle threw sand, she shifted the orientation of her body, and the indiscriminately flung sand gradually filled the nesting pit and sprinkled the surroundings through a radius of 6 to 8 feet. As the pit filled, the shifting stopped, but the scooping and throwing of sand with the fore fins continued, and eventually produced two good-sized basins (one for each flipper) at some distance from the former rim of the now indistinguishable nest excavation. Gradually the scattering of sand was discontinued, and the turtle began shuffling and scuffing about over and near the site (but doing nothing like the pounding mentioned

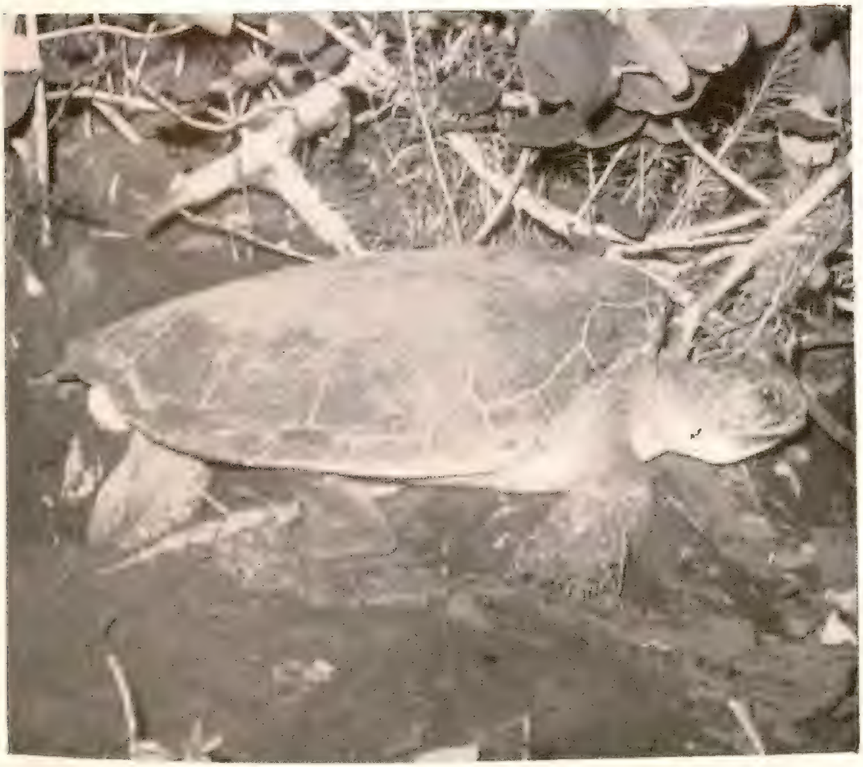

FIG. 13. Green turtle filling her nest after laying. This individual (not the one involved in the accompanying description of laying) went through the whole nesting process perched on a root that was too strong for her to break out of her broad nest depression and that prevented her sinking into it in the usual way.

in the literature on other species). When all work was done the two depressions scooped out during the filling process by the fore flippers remained as the most conspicuous features of the local topography and may reasonably be regarded as diversionary in function.

At 11:32 P.M. all concern with the nest seemed to leave the turtle suddenly, and she made for the sea, moving towards it at an angle of roughly 20 degrees and disappearing in the surf at 11:43 P.M.

The features of the behavior of the above individual (shown by other observations to be characteristic) that represent departures from the nesting pattern of the loggerhead and the ridley are: (1) the peculiar striking of the shell margin by the off foot during the digging of the egg hole; (2) the very different position of the back fins during oviposition; (3) the leaving of diversionary pits; and (4) the (often) protracted period of "smelling" of the submerged or wet sand before emerging (see below). In view of the uncertainty of evaluations of relationships among sea turtles on morphologic grounds, it will be of great interest to see how the hawksbill, a form about which little of significance has been published, aligns itself with respect to nesting pattern.

STRANDING CUES: Interpretation of our observations in terms of possible orientation cues evoking the stranding response is not easy. It is as hard to understand how turtles know Tortuguero when they arrive there as to understand how they are guided through the long distances they travel from their feeding ranges to Costa Rica. Certainly much, if not most, of the population is transitory. Its reaching Tortuguero must involve, as well as equipment for navigation, some mechanism for "recognizing" good nesting shore (in this case Tortuguero) when it is reached.

Probably hydrologic factors are involved. It may be only a matter of the distribution and strength of long-shore currents, although these appear to vary erratically (as well as seasonally). Perhaps the distribution of fresh-water masses off the mouths of the Costa Rican rivers (either operating directly or by excluding some important stenohaline predator of baby turtles), or even such trivial things as the drifting mats of water hyacinths from the rivers, which could be a concealment opportunity for newly hatched young, are guideposts. Or possibly merely a certain degree of fatigue tells the turtles they are off the right section of the shore.

There is no doubt that a tendency towards clumped arrivals exists. Significantly more turtles come up on certain nights, or during a short period of the night, or on a certain short stretch of apparently homogeneous shore. As there seems to be little or no predictability or periodicity about these clumpings, they may be due to independent individual response to clumped favorable factors. On the other hand, the clumping may merely result from the gregariousness of the members of a migratory school, the occurrence of which is an assumption in foregoing discussions of quantitative data. But in any case, the problem of how the nesting beach is recognized remains.

The one overt sign that senses are consulted by the turtles in their coming ashore is their behavior when they go aground in shallow water shoreward of the breaker line. At this point a Caribbean green turtle habitually stops, bends her neck sharply downward, bringing her snout in contact with the bottom or with the wet sand and holding it there for as long as a minute, or sometimes even longer. It is exactly as if she were making an olfactory or gustatory evaluation of the shore as nesting ground.

On many occasions we have watched a turtle come out of the surf, stop when her plastron grounded and, for as long as 15 minutes, alternately "smell" the sand (sometimes under a foot or so of water, sometimes well above wave reach), then raise her head high and move it slowly about as if in myopic study of the prospect. Often these periods of appraisal end abruptly, with the return of the turtle to the sea, as if the shore had been found unsuitable. Other times the "smelling" may continue at intervals all the way up to the zone of loose dry sand, where it is discontinued.

Carr has described elsewhere (1954a, 1956) an aerial reconnaissance of the shore south of Tortuguero where he saw on a 6-mile section of beach hundreds (perhaps thousands) of the short, V-shaped trails made by turtles that have not nested, or even gone up beyond high-tide line, but merely have come a few feet up from the waves, prospecting. In this case all the tracks had been laid down during one night. The inference is that a migratory school was passing, and one can imagine the cruising hosts, singly or by squads, turning in to the shore from time to time to test the ground with their noses, "meditate," and then move on northward towards whatever they sought in the way of a more reassuring substrate.

Whatever the nature of the responses that bring the female green turtle ashore, in the last stages of stranding, at least, some delicate discriminatory process seems to be involved. We have seen evidence that one turtle may make three or four, and possibly a good many more, painstaking appraisals at points along a section of beach, eventually either accepting the site as good for laying or moving away to try elsewhere or to await another night. The strong negative response to light was mentioned above. We have, experimentally, often sent an emerging turtle scurrying back into the water by one flick of a flashlight beam across her eyes. The *veladores* say lighting a cigarette at the coco-plum line sometimes scares away a turtle coming out of the surf. A man or dog moving between the turtle and a luminous horizon shoreward has the same effect. In this way, the green turtle seems clearly more impressionable than the loggerhead, and one is tempted to see this heightening of stranding responses and adjustments as one of the necessary adaptive concomitants of massed migratory breeding, with its complex chain of orientation reactions.

Balancing this fastidiousness in making the stranding "decision" is an incongruously dogged stubbornness in the drive to lay, exemplified by the return (see above) to the beach of No. 227 only a few hours after the experience of spending a night on the beach on her back. Comparable cases are numerous in our records, as is shown by the first peak in the curve in figure 9. Females often come ashore dragging with them much larger males attempting copulation. That these are not merely desperately fleeing unwelcome attentions seems indicated by the fact that a female also frequently comes up hauling a log tied to her fore flipper with a rope 6 or 8 feet long. To get turtles out to the launch that takes them to market, the *veladores* tie a wooden buoy to the fin of each turtle and make her swim to the coasting boat. Some of these escape, and they sometimes come back ashore and complete a laying venture with the log attached. We have what seems to be a reliable record of one of these escapees that was retaken at Bocas del Toro, nearly 200 miles away.

Whatever may be the nature of the senses used in coming to, and in recognizing, the beach the choice of the nest appears to be no more than the "feel" of the sand when trial scoops are made with the flippers. The turtle simply keeps going (in a direction determined by factors not well known) until she comes to an obstruction or until a few trial scrapings of the sand satisfy her. Obstructions that stop her may be dunes, vegetation, or a storm-thrown log. Any of these will probably be located above the reach of normal high tide and thus in good nesting sand, and, as a prospecting turtle usually stops and tries the sand when she meets such an obstacle, a majority of nests are found in such places.

In the case of the broad, duneless bars or spits near the river mouths, where no vegetation grows, turtles sometimes go considerable distances, sometimes as far as a quarter of a mile, in search of good ground. On the low, wide bar between the lower end of the Tortuguero River and the sea, tracks often show that turtles have pushed the futile search for deep nesting sand clear across the peninsula and, on reaching the river bank, have parted the hyacinths and entered the river.

It is of interest that the relatively small number of hawksbill trails we have seen seem to indicate a far greater tendency in that species to wander in its search for a nesting place.

Courtship and Copulation: Mating occurs (mainly, perhaps almost exclusively) off the nesting beach, as is known to be true of the Pacific form. Whether it takes place before or after laying, or both, is not known. Certainly males often head for females as they go back into the sea, but no actual copulating has been observed to result at such times. Both of us have seen females come ashore dragging, or pursued by, males, as we mention above. Harrisson (1954) said, with regard to this point, "It looks to me as if it [copulation] mainly occurs *after* the female has laid," but he gave no evidence.

Pairing is a strenuous and clumsy operation, and the female often ends an outing at the beach in bad shape—gashed, scraped, and with deep notches broken out of the fore margin of her carapace, one on either side of her neck, where the grappling nails of the male have clawed for support. Prior to pairing there is often considerable confusion that seems to be fighting between males, but may be the striving of rival suitors to mount a female simultaneously. Carr has elsewhere (1956) mentioned the frequency with which groups of three floating turtles (a female and two attendant males) may be seen from the air off the beach in the nesting season. It is of interest that Harrisson *(loc. cit.)* refers to similar observations for the Pacific green turtle.

When pursuing or trying to mount the female, a male green turtle is apparently oblivious to all other stimuli. When the *mancuernas,* as the mated pairs are called, appear close inshore, the Tortuguero boys grab irons, run out into the surf, and sometimes succeed in harpooning the male before he is aware of their presence.

During the 1955 season, courting or mated green turtles, sometimes several in an afternoon, were seen frequently during early and middle July. Towards the end of July such pairs appeared less often, and during all of August no sign of courting or copulation was observed.

ACKNOWLEDGMENTS

Aside from the sponsorship of the National Science Foundation (a *sine qua non* for its realization) this study has had support and cooperation from a number of sources.

The Limon personnel of Compañia Bananera de Costa Rica has, during four seasons, been unfailingly helpful.

Señor Teodoro Quirós C. has for the same four seasons placed at the disposal of the investigation the facilities of the timber and banana station of the Atlantic Trading Company at Tortuguero. In the Limon office of that enterprise, Mr. Stanley Lettman has been consistently cooperative.

The work on the beach was greatly facilitated by the courtesy of the Costa Rican Ministry of Agriculture, which provided aid from local conservation officials and placed at our exclusive disposal the 2-mile section of Tortuguero Beach between the settlement and the mouth of the river.

In San José Mrs. Doris Stone was of assistance in arranging for field work, and Dr. Rafael Lucas Rodríguez of the University of Costa Rica furnished valuable advice and encouragement.

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The original decision to work at the Tortuguero site was reached after reconnaissance travels supported by a grant from the American Philosophical Society.

From its earliest state to the present, the work has received wholehearted cooperation from the captains and crews of the Cayman turtle fleet and from the people of the Cayman Islands generally.

To all the above, and to the literally hundreds of fishermen all about the Caribbean, whose talk lent form to conceptions that led up to the study, we are naturally extremely grateful.

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